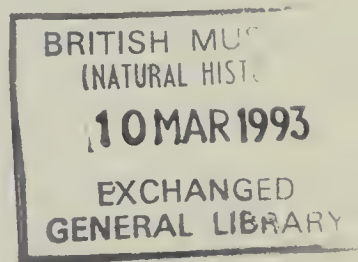


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A myriacanthid holocephalan (Chondrichthyes) from the Sinemurian (Lower Jurassic) of Osteno (Lombardy, Italy)

Riassunto — Un olocefalo miriacantide (Chondrichthyes) del Sinemuriano (Giurassico inferiore) di Osteno (Lombardia, Italia).

Viene descritto un esemplare di olocefalo miriacantide del Sinemuriano (Giurassico inferiore) di Osteno (Lombardia). Il condocranio e la mandibola sembrano privi di placche dermiche. Il clasper è lungo circa la metà del rostro e nella parte ventrale presenta una superficie dentellata per due terzi della sua lunghezza. La cartilagine di Meckel, poco profonda, è situata piuttosto in avanti. La dentatura superiore comprende un paio di lunghe lamine dentarie posteriori e almeno un altro paio di lamine anteriori, mentre nell'arcata inferiore è presente un solo paio di lamine dentarie. L'esemplare italiano è distinguibile da *Myriacanthus*, *Metopacanthus* and *Acanthorhina*, anch'essi determinati sulla base di resti cranici. Le lamine dentarie non possono essere adeguatamente comparate con quelle di altri generi di miriacantidi, per cui la nomenclatura del materiale di Osteno è ancora aperta.

Abstract — A single specimen of a myriacanthid holocephalan is described from the Sinemurian (Early Jurassic) of Osteno (Lombardy). Dermal plates seem to be lacking on the chondrocranium and mandible. The frontal clasper is approximately half the length of the rostrum, with the ventral surface denticulate for two thirds of its length. The short deep Meckel's cartilage is placed well forward. The upper dentition comprises a pair of long posterior tooth plates and at least one pair of anterior tooth plates. There is a single pair of tooth plates in the lower dentition. The Italian specimen is distinct from *Myriacanthus*, *Metopacanthus* and *Acanthorhina*, which are also known on the basis of cranial remains. The tooth plates cannot be adequately compared with those of other myriacanthid genera, so the Osteno material is left in open nomenclature.

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Key words: Chondrichthyes, myriacanthid, Sinemurian, Lower Jurassic, Lombardy.

Introduction

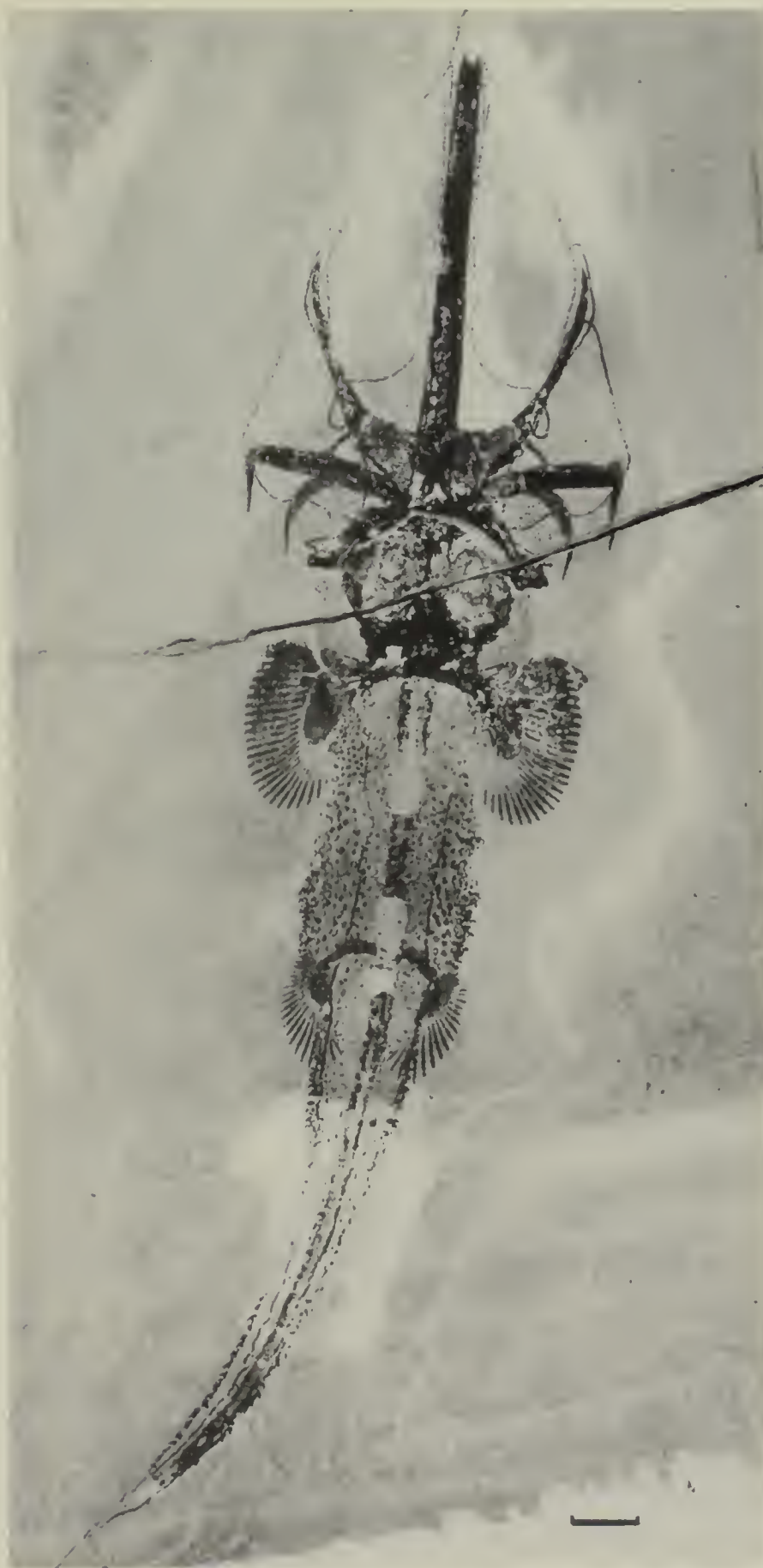
The holocephalans are a group of cartilaginous fishes which range from late Devonian to Recent. Those inhabiting modern seas include the colloquially named Ratfishes and Elephant fishes (eg. *Chimaera*, *Hydrolagus*, *Rhinochimaera*, *Callorhynchus*). All modern representatives are marine, and are found in both deep sea (around 2000 metres) and shallow shelf waters (less than 20 metres). The group shows characteristic sexual dimorphism; the male possesses mixipterygial pelvic claspers as in sharks, a pre-pelvic clasper or tenaculum, and a frontal clasper articulating with the ethmoid part of the chondrocranium. Although mating behaviour has not been observed, it is assumed that the pre-pelvic and frontal claspers, each with their ventral armature of pointed scales, are used to grip and stimulate the female. From the limited data available, modern chimaeroids appear to be opportunistic feeders, taking a wide variety of prey species including molluscs, crustaceans, annelids, echinoderms, cnidarians and fish at or near the sea floor (Duffin 1983a: 23; Ribbink 1971).

All extant holocephalans belong to the suborder Chimaeroidei, which extends back to the Late Pliensbachian (Early Jurassic), with the record of *Eomanodon simmsi* Ward & Duffin (1989). Coeval with the early chimaeroids, two further holocephalan suborders are known from the Early Mesozoic, both of which are represented by single specimens from the Sinemurian deposits (Early Jurassic) at Osteno, Lombardy.

The Squalorajoidei contains a single genus, *Squaloraja* Riley (1833). *Squaloraja polyspondyla* (Agassiz, 1836) is well known from the «Lower Lias» (Hettangian to Sinemurian) black shales of Lyme Regis, Dorset, on the south coast of England (Smith Woodward 1891, Patterson 1965, Duffin 1983a). The Osteno specimen (MSNM V655) (Arduini, Pinna & Teruzzi 1982 pl. 8 fig. 1) is complete, beautifully preserved and fully articulated, comprising part and counterpart, and showing details of the sensory canal system and squamation (Figure 1). The specimen is currently being described by Dr. Colin Patterson.

The Myriacanthoidei was erected by Patterson (1965) to encompass the myriacanthids (subsequently incorporating *Acanthorina*; Duffin 1983a) and chimaeropsids. The suborder contains 9 genera and 10 species, whose stratigraphic distribution is summarised in Table 1. Myriacanthids are distinguished by the possession of three paired upper tooth plates, a lower symphyseal and single pair of lower tooth plates, a large elongate rostrum, very large frontal clasper, a pair of tuberculated mandibular dermal plates, and a tuberculated dorsal fin spine.

The object of this paper is to describe a single specimen of a myriacanthid holocephalan, cited as *Metopacanthus* sp. by Schaeffer & Patterson (1984: 71, table 3), from the spongolithic micrites of Osteno, Lombardy.



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Table 1 – Table to show the stratigraphic and geographical distribution of Mesozoic holocephalans. The resolution for squalorajoids, myriacanthids and chimaeropsids is to species level, chimaeroids to genus only. For greater resolution in chimaeroids see Ward & Duffin (1989).

Table 1	Myriacanthidae												Chimaeropsidae			Squaloraja polyspondyla	Chimaeroidei						
	<i>Agkistracanthus mitgelensis</i>	<i>Alethodontus bavariensis</i>	<i>Recurvacanthus uniserialis</i>	<i>Halonodon warneri</i>	<i>Myriacanthus paradoxus</i>	<i>Metopacanthus granulatus</i>	<i>Metopacanthus bollensis</i>	<i>Metopacanthus</i> sp.	<i>Myriacanthid</i> indet.	<i>Acanthorhina jaekeli</i>	<i>Myriacanthid</i> indet.	<i>Chimaeropsis foussi</i>	<i>Chimaeropsis paradoxa</i>	<i>Chimaeropsis franconicus</i>	<i>Eomanodon simmsi</i>		<i>Ganodus</i> spp.	<i>Ischyodus</i> spp.	<i>Pachymylus leedsi</i>	<i>Brachymylus</i> spp.	<i>Elasmodectes secans</i>		
Key:																							
B - Belgium																							
D - Germany																							
F - France																							
GB - Britain																							
H - Switzerland																							
I - Italy																							
Country	H	D	GB	B	GB	GB	D	D	I	D	GB	B	D	D	GB I	GB	GB	GB D F	GB	GB	GB		
Portlandian													X	?				X					
Kimmeridgian																		X			X		
Oxfordian																							
Callovian																		X	X	X			
Bathonian																	X	X		X			
Bajocian											X							X					
Aalenian																							
Toarcian							X	X		X													
Pliensbachian																							
Sinemurian			X	X	X	X			X		X	X			X								
Hettangian	X	X																					
Rhaetian	X										X												

Systematic palaeontology

Class Chondrichthyes Huxley, 1880
Subclass Holocephali Bonaparte, 1832
Order Myriacanthoidei Patterson, 1965
Family Myriacanthidae Smith Woodward, 1889
Myriacanthid indet.
(Figures 2-7,10)

Specimen: MSNM V635.
Locality: Osteno, eastern shore of Lugano Lake, Como Province, Lombardy, northern Italy. Topographic map: Foglio Valsolda 17 III S.O., Longitude 0°3'36"E, Latitude N. 46°00'46".
Horizon: Spongolithic micrite, Lombardische Kieselkalk Formation, *Bucklandi* zone, Lower Sinemurian, Early Jurassic.

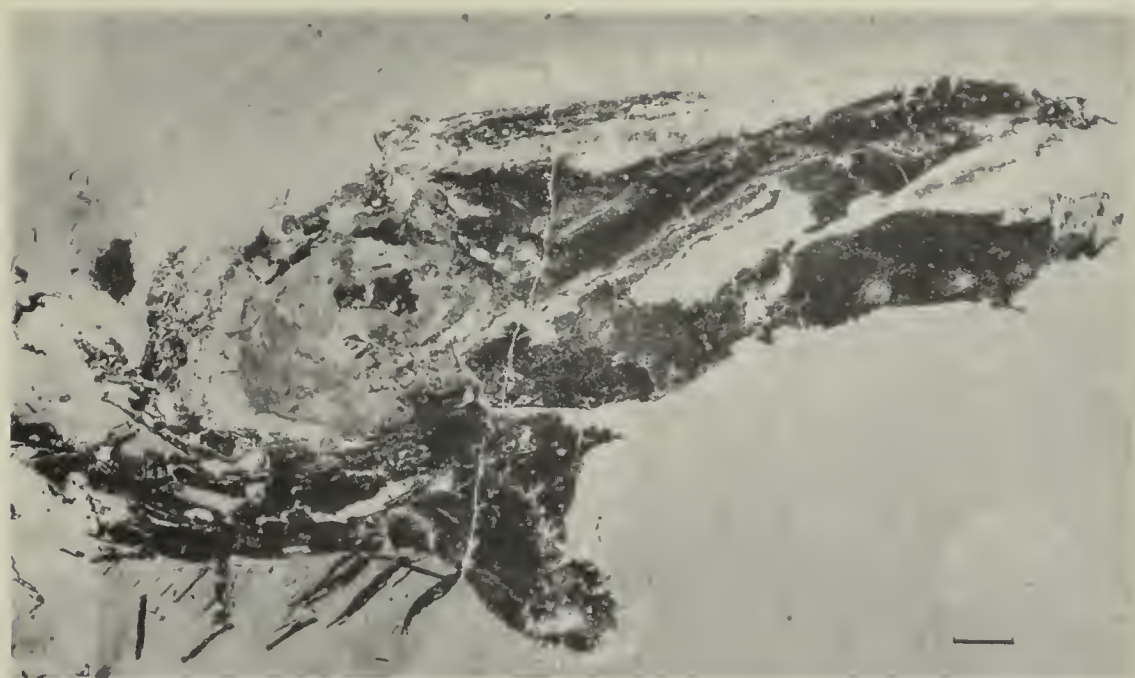


Fig. 2 - V635, a myriacanthid holocephalan from the Sinemurian (Lower Jurassic) of Osteno. The specimen presents a virtually complete skull with associated parts of the branchial skeleton in right lateral view. Scale bar = 10 mm.

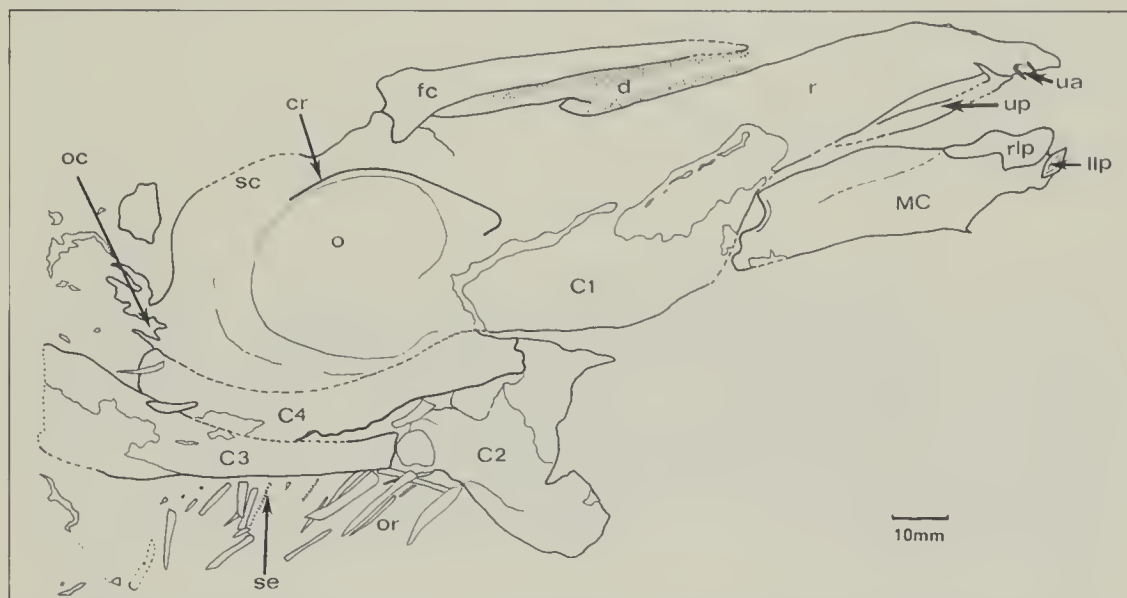


Fig. 3 - Outline drawing of V635 from the Sinemurian (Lower Jurassic) of Osteno, to show the suggested distribution of anatomical details described in the text. Scale bar = 10 mm.

Description

The specimen is preserved in right lateral view on a single block of hard grey micrite (Figure 2). Counterpart blocks are not available. The chondrocranium, lower jaw, parts of the dentition and ?opercular skeleton are preserved, together with some presently undetermined cartilage fragments.

The maximum preserved length of the specimen is 195 mm from the edge of the block to the tip of the rostrum. The chondrocranium measures 171 mm from the occipital region to the rostrum tip, and is covered by a tes-

serated arrangement of calcified prisms. The most prominent feature is the large subcircular orbit (abbreviated as «o» in Figure 3), which is 40 mm in length anteroposteriorly and 35 mm dorsoventrally. Traces of a circumorbital ridge (cr) can be discerned along the dorsal and parts of the anterior orbital margin. Representations of retinal pigment are present in the form of a dark (presumably phosphatised) area within the orbit (Figure 2).

The otico-occipital region of the chondrocranium is not very deep (the postorbital length is 14 mm). The occipital cotylus (oc) cannot be distinguished directly, but its position can be inferred from the backward sweep of the posterior chondrocranial margin. The suborbital depth is around 12 mm. Part of a moderate sagittal crest (sc) is developed above the occipital cotylus.

The rostrum (r) is quite robust and elongate, extending 110 mm in front of the orbit. It is straight and narrows distally to a moderate point. The dorsal and ventral margins are virtually entire, although small areas of cartilage are missing. The dorsal rostral margin is slightly convex distally and the ventral rostral margin (vm) is concave for the insertion of the upper dentition.

The frontal clasper (fc) is preserved in slightly oblique dorsal view and is assumed to be in life position, based upon the distribution of opposing denticles on the dorsal rostral margin. Its origin is above the anterior third of the orbit (Figures 2, 3). Proximally, the base is spatulate, measuring 12 mm in width. This expansion of its articular extremity was to allow the insertion of depressor musculature. The structure is densely calcified and extends forward in a straight line for at least 67 mm - almost exactly half the total length of the rostrum. The distal tip is missing and is presumably on the (unavailable) counterpart. A jumbled, slightly displaced mass of denticle bases and downturned, often broken crowns is located 8 mm anterior to the

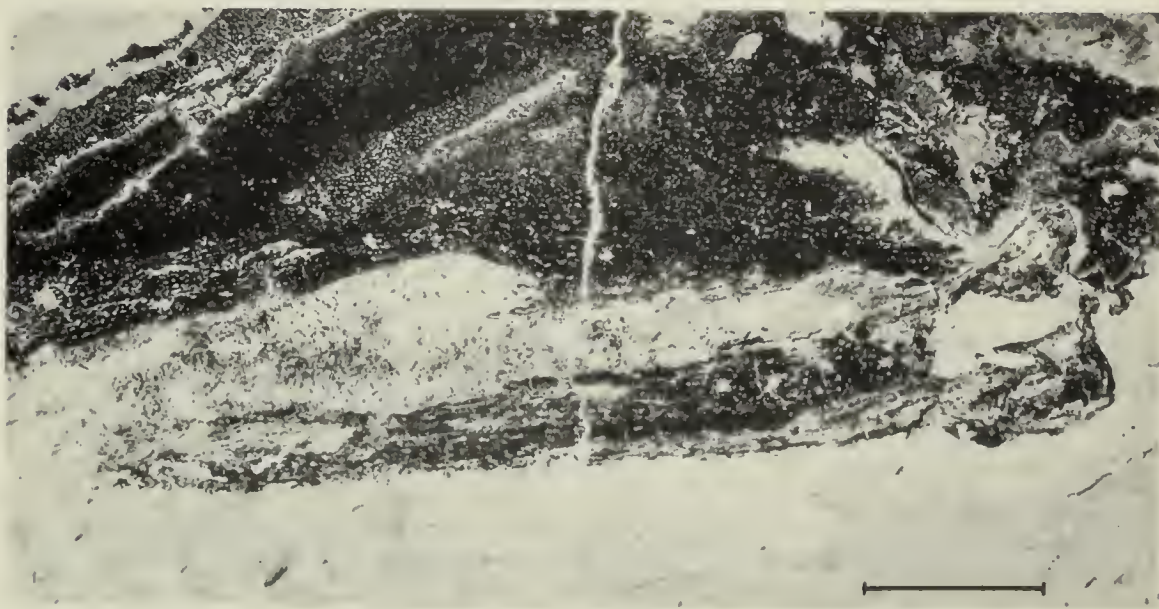


Fig. 4 - The frontal clasper and dorsal margin of the chondrocranium and rostrum of V635 from the Sinemurian (Lower Jurassic) of Osteno. Note the straightness of the frontal clasper, the spatulate articular base, and denticulate ventral surface with opposing denticles on the rostrum. Scale bar = 10 mm.

frontal clasper shaft (Figures 4, 5). The attitudes of the denticles imply that they are from the clasper tip.

The ventral side of the clasper is ornamented by a densely packed series of denticles (Figures 4, 5). Each denticle consists of a 1 mm wide flared base surmounted by a slightly recurved, sharply pointed cusp with circular cross section. The maximum height of the denticles is 2 mm. The denticulate portion extends for the distal two-thirds of the clasper undersurface. There is no evidence for the presence of similar or larger denticles on the dorsal clasper surface.

The clasper denticles are opposed by closely similar structures along the dorsal rostral margin (Figures 4, 5). The rostral denticles commence some half way along the frontal clasper length. Occasional large denticles (d) are present anterior to the frontal clasper along the dorsal rostral margin, the most anterior being some 20 mm behind the rostral tip.

Parts of the upper dentition are visible in oblique and lateral views (Figures 2, 3). Patterson (in press) has recently reviewed the interpretation of chimaeroid toothplates, and his revised terminology is followed here. A long (32 mm) strip of densely calcified lamellar tissue, partially obscured by sediment, is all that is visible of the labial wall of the right upper posterior tooth plate (up) («palatine»). Part of the symphyseal margin can be discerned anteriorly (Figure 6). This is preceded anteriorly by a 3 mm long ventrally-projecting strip of the root wall (the descending lamina; Patterson in press) forming the posterior margin of the right upper anterior tooth plate (ua) («vomerine»). The impression was gained from the specimen that the labial and symphyseal margins are also present (Figure 6), together with traces of the base of its pair. The anterior tooth plate would have measured 2 mm anteroposteriorly. There is room on the ventral rostral margin to accommodate a further anterior tooth plate, of which a small section of the descending lamina may be present (Figure 6).

Parts of the lower dentition are preserved in a direct occlusal relationship with the upper tooth plates, and remain attached to the Meckelian

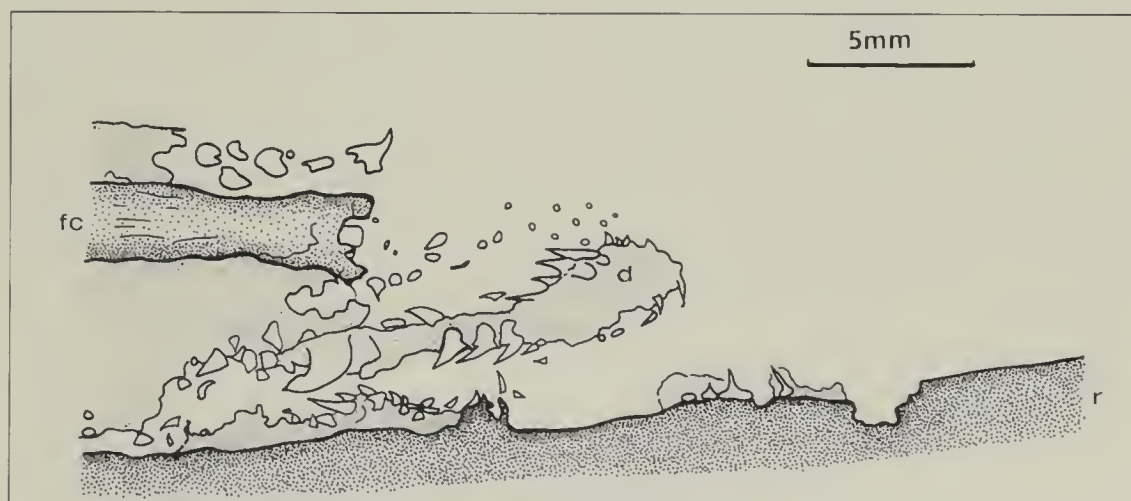


Fig. 5 - The distal portion of the frontal clasper of V635. Note the broken downturned cusps and denticle bases forward of the clasper shaft, implying the position of the clasper tip. Scale bar = 5 mm.

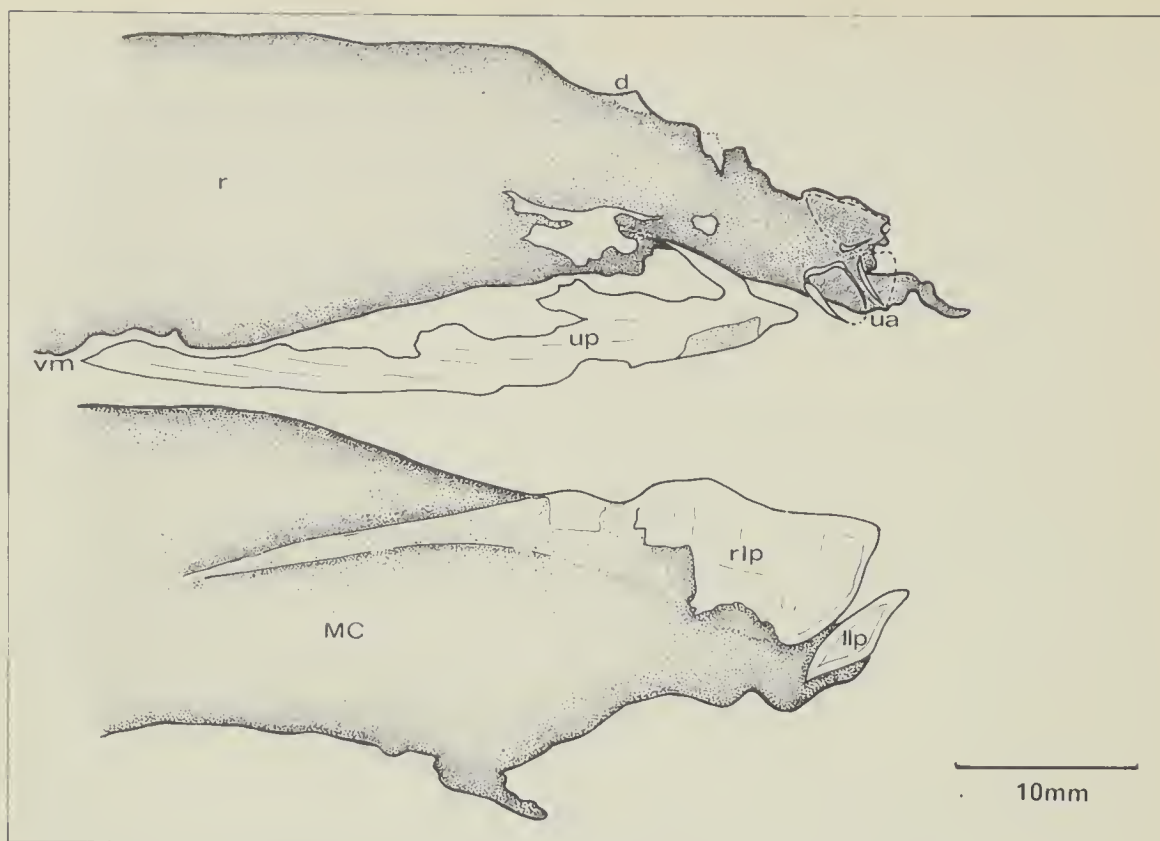


Fig. 6 - Camera lucida drawing of the dentition of V635 (Sinemurian of Osteno). Scale bar = 10 mm.

cartilage (MC) which forms the lower jaw. The 20 mm long undulating occlusolabial margin of the right lower tooth plate (rlp) is clearly defined. This outline suggests the presence of strongly developed symphyseal ridge and at least one diagonal ridge on the occlusal surface of the tooth plate. The posterior part of the labial wall of the right lower tooth plate can be made out as a thin ridge produced by differential compaction of the jaw cartilage. This suggests that the tooth plate would have been around 46 mm in total length. A 2.5 mm high upright strip of lamellar tissue represents the mesial angle of the symphyseal margin of the left lower tooth plate (llp), and is situated just in front of the right lower tooth plate.

There is no sign of a symphyseal tooth plate on the block, and X-ray photography (negatives held by the Museo civico di storia naturale in Milano) failed to reveal it enclosed by the sediment. It is possible that a symphyseal tooth plate was present but located on the counterpart, but my feeling from the way in which the Meckelian cartilage has been broken is that its absence is real, rather than an artefact of preservation.

None of the tooth plates preserved on the specimen is exposed in such a way as to reveal the pleromin of the occlusal surface.

The crushing of the skull cartilages introduces some difficulties when it comes to interpretation of the Meckelian cartilage. The lower jaws of extant chimaeroids and fossil myriacanthids and squalorajoids are characteristically short and deep, with approximately two-thirds of the length taken up with the lower dentition. The Meckel's cartilage in V635 is 14 mm deep at the

tooth plate. This is almost identical to the rostral depth at the same location. 56 mm behind the symphysis the cartilage shows a deep double embayment. This appears to be a real boundary, rather than a break, and if interpreted correctly would represent the articular surface at the proximal end of the lower jaw. The proportion of the cartilage occupied by the right lower tooth plate supports this conclusion.

Between Meckel's cartilage and the orbit is a long (54 mm), deep (22 mm) badly crushed and broken cartilage (C1). In places, this cartilage is continuous with the rostrum, and is interpreted here as the distorted remains of the deep proximal part (quadrate region) of the rostrum itself. There is no evidence of an articular surface corresponding to that at the back of the lower jaw.

The above determinations raise the question of the identity of a large mass of cartilage (C2) situated anterior and ventral to the orbit. This structure is a complex of broken and partly overlapping cartilage fragments which appear to show some continuity with the chondrocranium. Perhaps this is the highly distorted pair to C1. Alternatively (and more likely), since the opercular rays (described below) are directed away from this structure, it may represent crushed parts of the hyomandibula and hyoid. Further specimens are needed to elucidate these structures.

There is no sign of sensory canals overlying the prismatic cartilage of the skull. Two small lengths of sensory canal (se) are preserved some 30 mm ventral and slightly posterior to the orbit (Figure 7). The canals are surrounded by incompletely circular calcified rings measuring 0.6 mm across. The two strips measure 13.5 mm and 8 mm in length, comprising approximately 32 and 30 visible canal rings respectively. The strips are sub-parallel, only mildly disarticulated along their lengths, and probably represent symmetrically arranged parts of the mandibular canal (jugular or jugal canal of earlier authors) from the right and left sides.

The presence of the sensory canals means that the series of elongate cartilage strips closely associated with them must be from the gill area, rather than pectoral fin radials. The cartilages in question are all elongate and roughly rectangular. They measure up to 16 mm long and 1 mm across, although some are only 6 mm in length. They are all sub-parallel to each other (Figure 3). These cartilages seem insufficiently massive to be the ceratobranchials, pharyngobranchials and epibranchials of the gill arch skeleton. The more likely interpretation is that they are the fine «rays» («radien» of Schauinsland 1903) which extend posteriorly in a branching network from the hyomandibula and hyoid to form the operculum.

Just beneath the ventral border of the chondrocranium are the crushed remains of some rather more robust cartilages. Of these, C3 and C4 are probably remains of the scapulocoracoids, with the right (C3) partially overlying the left (C4). If this interpretation is correct, the scapulocoracoid would have been at least 66 mm in length and 15 mm wide, although further morphological details are lacking (Figure 3).

Some further incomplete traces of cartilage behind the chondrocranium probably represent parts of the synarcual, and perhaps the basals for the dorsal fin. There is no sign of any notochordal sheath calcifications or the dorsal fin spine.

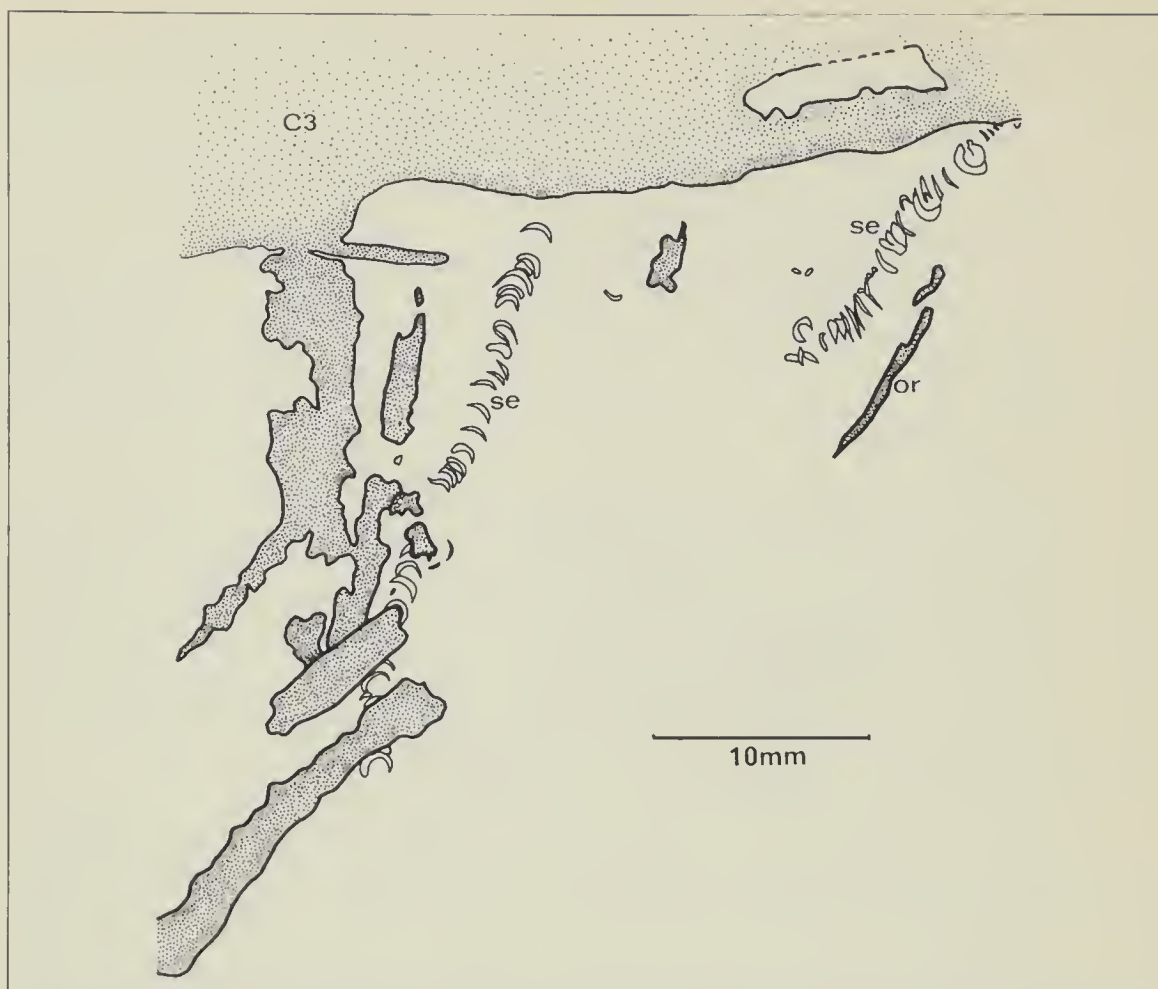


Fig. 7 - Camera lucida drawing of parts of the opercular skeleton and lengths of sensory canal (?mandibular) in V635 (Sinemurian of Osteno). Scale bar = 10 mm.

Discussion of affinities

The holocephalan identity of the specimen is evident from the overall form of the dentition and chondrocranium. Amongst Mesozoic holocephalans, V635 could only belong to a myriacanthid because of the large robust frontal clasper found in conjunction with tooth plates which bear diagonal ridges (inferred from the form of the labial margins of the tooth plates). By contrast, chimaeroids possess tiny frontal claspers and tooth plates on which variation in relief is achieved by the presence of tritons. The frontal clasper of squalorajoids is similar to that of myriacanthoids, but the tooth plates do not possess diagonal ridges.

Amongst the myriacanthids, *Myriacanthus paradoxus*, *Metopacanthus granulatus*, *Metopacanthus* sp. (Reif 1974) and *Acanthorhina jaekeli* are represented by complete or partial skull material. The skull of *Myriacanthus paradoxus* is incompletely known (Agassiz 1836, Smith Woodward 1891, 1906, Dean 1906, Patterson 1965) but is believed to have been dorso-ventrally flattened (Patterson 1965: 128). The skulls of *Metopacanthus* and *Acanthorhina*, like V635, are laterally compressed (Figures 8a, b), as is that of *Chimaeropsis* (Figure 8c).

The presence of tuberculated dermal plates is characteristic of myriacanthids and chimaeropsids. Reis (1895) reconstructed *Chimaeropsis para-*

doxa with three pairs of dermal plates, one on the crest of the synarcual, one on the posterior part of the sagittal crest, and the final pair posterior and ventral to the orbit (Figure 8c). No dermal plates are known from *Squaloraja* or the chimaeroids. *Myriacanthus paradoxus* possessed a pair of dermal plates, one at the postero-lateral extremity of each mandibular ramus. The plates are ornamented with rows of weakly ridged tubercles, and terminate in up to four recurved spines (cf. BMNH P. 4664, Figure 9a). At least 3 further asymmetrical paired dermal plates were present (Smith Woodward 1906, Patterson 1965). The most likely positions of these additional plates are on the dorsolateral corners of the occiput, just behind the insertion of the frontal clasper, and possibly the ventro-lateral corner of the occiput (Patterson 1965: 131). Tuberculated dermal plates are also known from the ventro-lateral corner of the mandible, just behind the insertion of the frontal clasper, and possibly on the dorso-lateral corner of the occiput in *Acanthorhina jaekeli* (Duffin 1983a). *Metopacanthus granulatus* appears to have possessed only one pair of dermal plates, situated in the angle of the mandible (Patterson 1965; Figure 9b). Although typically myriacanthid in other respects, V635 shows no sign of any dermal plates anywhere on the specimen, and their presence is not indicated by X-ray photography. It is unlikely that they have been lost during fossilisation and collecting, given the overall state of preservation of the material.

The rostrum of *Metopacanthus granulatus* is elongate, broad and heavily calcified, ending in a «hoe-shaped» tip (Figure 8b). Although incompletely known, that of *Myriacanthus paradoxus* appears to be of similar size and shape (Patterson 1965: 129). That in *Acanthorhina* is slightly shorter in relation to overall skull length, is straight and narrows evenly to a sharply pointed tip (Duffin 1983a; Figure 8a). The rostrum in V635 remains deep for the greater part of its length. Its tip is beak-like rather than hoe-shaped.

The upper dentition is confined to the immediate preorbital, proximal part of the rostrum in *Metopacanthus*, *Myriacanthus* and *Acanthorhina* (Figure 8), but is placed in a uniquely distal position toward the rostral tip in V635.

The dorsal margin of the rostrum is concave in *Metopacanthus* for the reception of the quite strong ventral curvature of the frontal clasper (Figure 8b). The clasper is similarly curved in *Halonodon warneri* (Duffin 1984). The details of this area of the rostrum are unknown in *Myriacanthus*, and the frontal clasper is incomplete in *Acanthorhina*. In V635, however, the dorsal rostral margin is virtually straight, as is the frontal clasper.

The form of the frontal clasper in the Italian specimen is unlike the much more robust, distally expanding fragment displayed by *Acanthorhina* (Duffin 1983a). The frontal clasper is sub-equal to the length of the rostrum in *Metopacanthus*, and probably of similar proportions in *Myriacanthus*. In V635, however, the clasper extended for just over half the length of the rostrum.

Only the proximal half of the clasper undersurface bears denticles in *Metopacanthus* and *Myriacanthus*, while two thirds of the ventral surface is denticulate in the Italian specimen. Details are lacking for *Acanthorhina* and *Halonodon*. As in *Metopacanthus* and *Myriacanthus*, sparse larger denticles are present on the distal part of the dorsal rostral margin in V635.

The mandible is slightly longer relative to the rostrum in V635 than in *Metopacanthus*, *Myriacanthus* and *Acanthorhina*. Also, it is positioned much further forward than in the other three genera, occluding against a terminally located upper dentition.

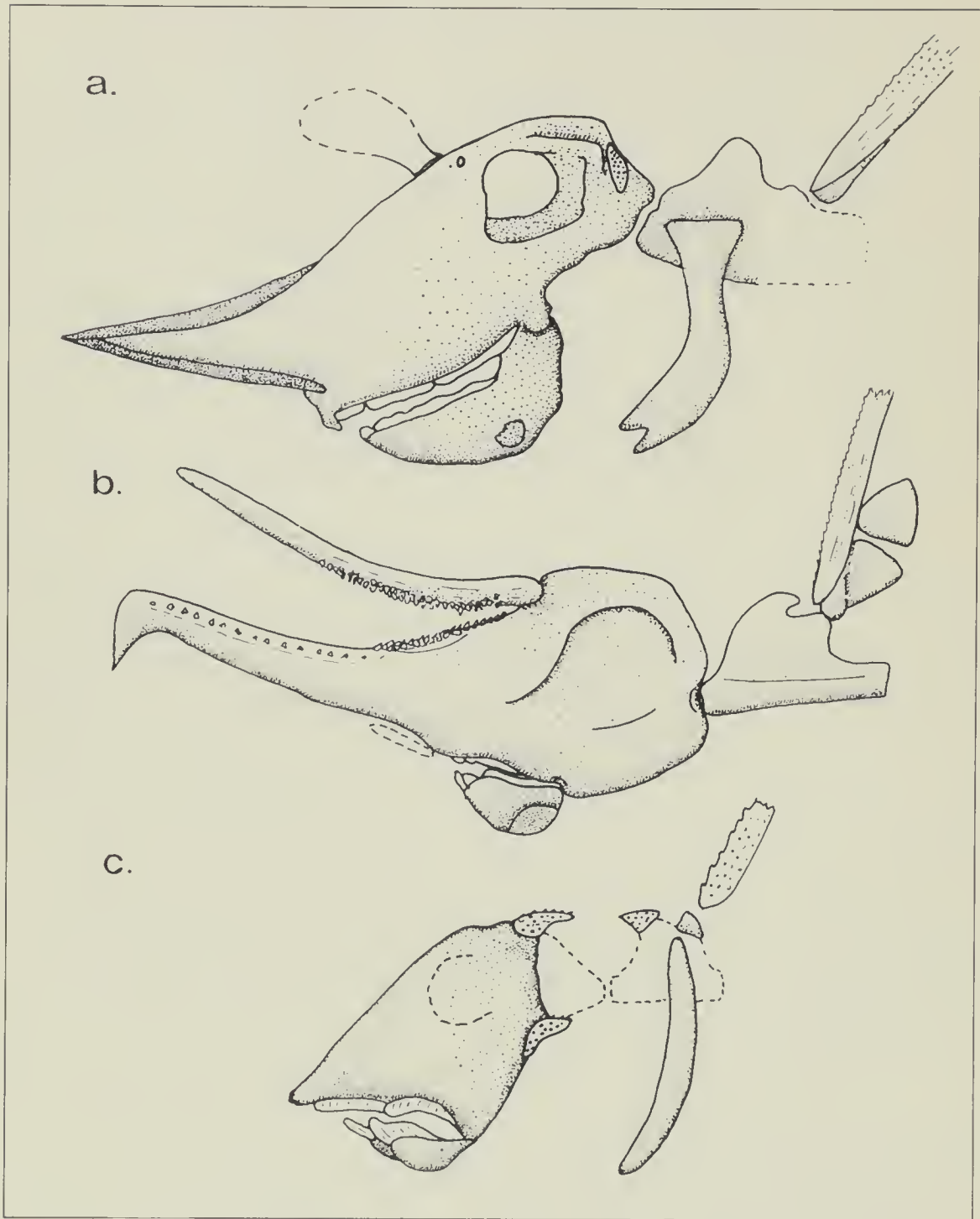


Fig. 8 – Outline reconstruction of a) *Acanthorhina jaekeli* Fraas (1910) from the Posidonienschiefer (Toarcian, Lower Jurassic) of Holzmaden, southern Germany (after Duffin 1983a); b) *Metopacanthus granulatus* Agassiz 1837 from the «Lower Lias» (Sinemurian, Lower Jurassic) of Lyme Regis, Dorset, England (after Patterson 1965); c) *Chimaeropsis paradoxa* Zittel (1887) from the Plattenkalk (Tithonian, Upper Jurassic) of Solnhofen, southern Germany (after Reis 1895).

There is no sign of the paired pre-mandibular cartilages found in *Myriacanthus* (cf. Patterson 1965 fig. 13), or any accessory or labial cartilages in V635.

The dentition consists of a large pair of upper posterior («palatine») tooth plates, at least one pair of upper anterior («vomerine») tooth plates, and a single pair of lower («mandibular») tooth plates in V635.

The lack of a lower symphyseal tooth plate contrasts strongly with the condition in *Myriacanthus*, *Metopacanthus*, *Acanthorhina* and *Halonodon*. Although it is conceivable that the element has been lost or is on the counterpart the preservation of the cartilage in this region of the Osteno specimen suggests that the lack may be real rather than artefactual.

The ratio of skull depth to length is 1:3.66 in the Italian specimen, as compared to 1:1.73 in *Acanthorhina* and 1:2.28 in *Metopacanthus*.

Thus, the specimen from the Sinemurian of Osteno differs considerably from all other Mesozoic holocephalans in which skull material is known. It can be placed with the myriacanthids on the basis of the long robust rostrum, well developed frontal clasper and the overall form of the dentition. It is unique in skull proportions, details of the rostrum and frontal clasper, the lack of tuberculated dermal plates, and the anterior location of the upper dentition and Meckelian cartilage.

V635 can only be meaningfully compared to 3 myriacanthid genera (*Myriacanthus*, *Metopacanthus* and *Acanthorhina*); the remaining 6 are defined on characters of the dentition or dorsal fin spine, details of which are currently lacking in the Italian material. As a result, I prefer to leave V635 in

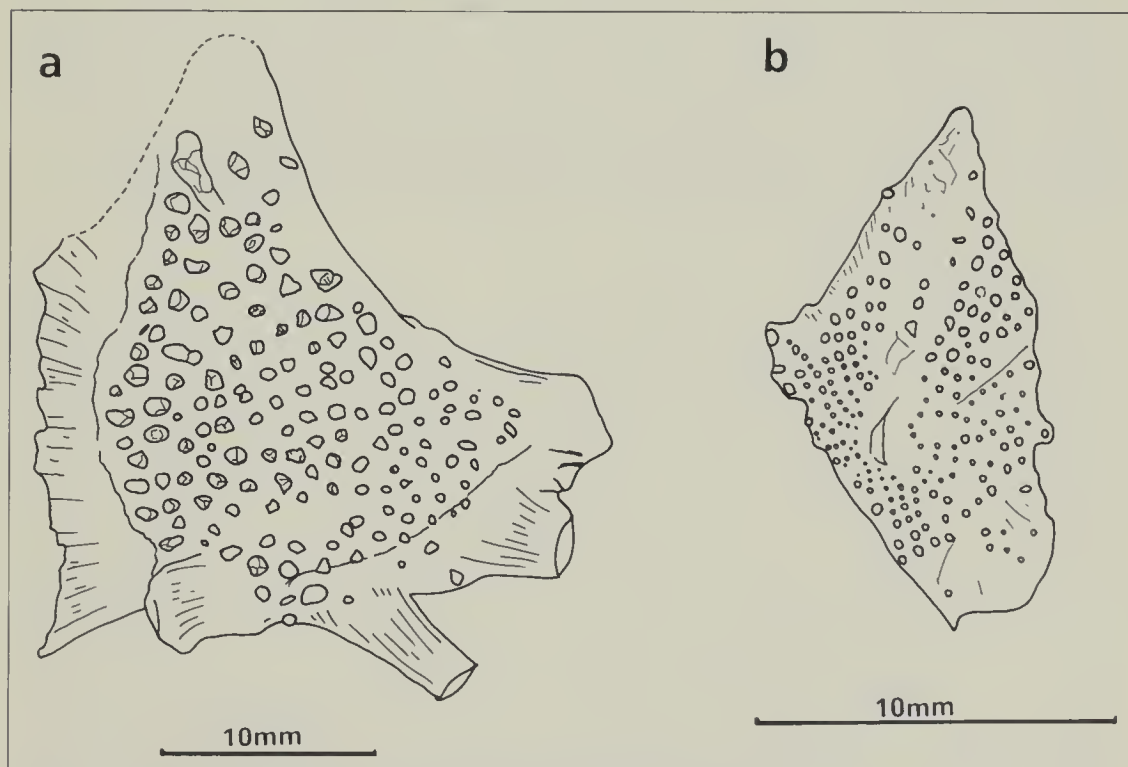


Fig. 9 - a) Camera lucida drawing of the left mandibular dermal plate of *Myriacanthus paradoxus* Agassiz (1836) from BMNH P. 4664 (Lower Lias of Lyme regis, Dorset, England). Bar scale = 10 mm. b) Camera lucida drawing of a dermal plate of *Metopacanthus granulatus* Agassiz (1837) from BMNH P. 1158 (Lower Lias of Lyme Regis, Dorset, England). Bar scale = 10 mm.

open nomenclature. My feeling is that, with future, more complete specimens, the Osteno myriacanthid will be shown to belong to a new genus.

An initial attempt at a reconstruction of MSNM V635, with operculum removed, is given in Figure 10.

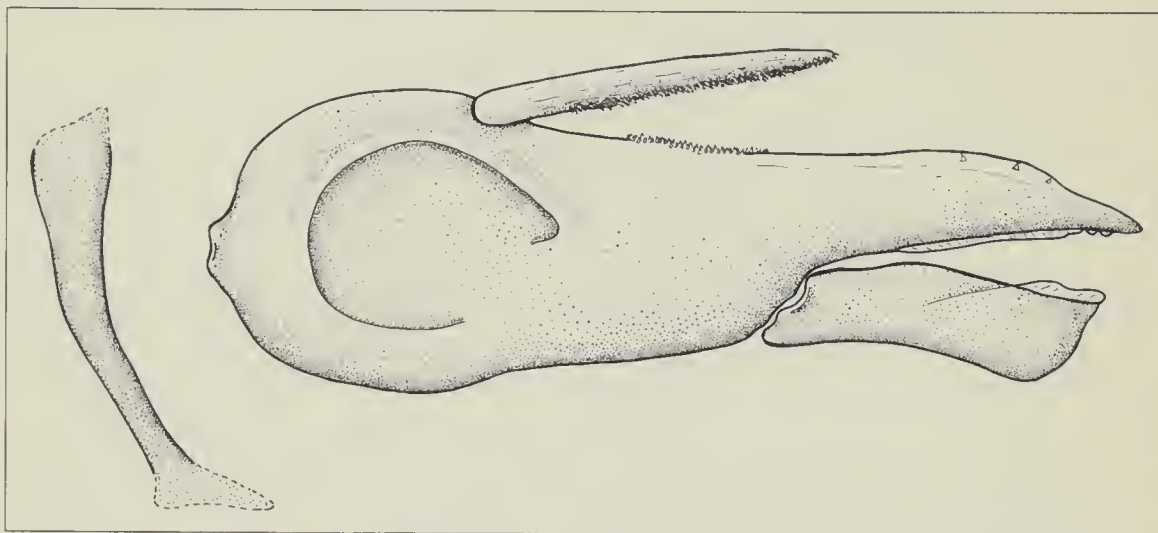


Fig. 10 - Preliminary outline reconstruction of V635, a myriacanthid holocephalan from the Sinemurian (Lower Jurassic) of Osteno, Lombardy (Italy). The operculum has been omitted.

Palaeoecology

MSNM V635 forms part of a low diversity Lagerstätte fauna which is believed to have been preserved in an isolated marine basin (Pinna 1985). The fauna contains decapod, hoplocarid and thyacocephalan crustaceans, coleoid and ammonoid cephalopods, polychaete and nematode worms, ophiuroid echinoderms, bivalves, brachiopods, drifted terrestrial plant remains, actinopterygian and coelacanth osteichthyans, squalorajoid holocephalans and the neoselachian shark *Palaeospinax pinnai* (see Duffin 1987 for a guide to the literature).

Myriacanthids have a crushing dentition. The occlusal surface of the robust, continuously growing tooth plates is covered with pleromin, a specialised tissue comprising closely packed denteon pillars oriented vertically (Ørvig 1985). Variation in surface relief is achieved by the development of diagonal ridges over the occlusal surface, lending a shearing component during biting. Mandibular adduction was achieved by contraction of the complex levator mandibulae musculature which had its origin pre-orbitally in the ethmoid region of the braincase and proximal part of the rostrum, as in chimaeroids (Edgeworth 1935). Duffin (1983a) suggested that *Acanthorhina* may have been capable of feeding on endo- and epibiontic invertebrates such as crustaceans, annelids and echinoderms, as well as nektonic invertebrates such as belemnites and ammonites. Assuming similar opportunistic feeding behaviour, potential prey species for the myriacanthid within the Osteno fauna could include the polychaete *Melanoraphia maculata* Arduini, Pinna & Teruzzi (1982), a variety of crustaceans (*Coleia* spp., *Glyphea*, *Pseudoglyphea*, *Mecochirus*, *Eryina*, *Aeger* spp.; Pinna 1968), phragmoteuthid coleoids and the ammonites *Ectocentrites*, *Sulciferites* and *Coroniceras* (Arduini, Pinna & Teruzzi 1982). Calcareous benthos is virtually unknown at Oste-

no, due to the diagenetic environment (Pinna 1985).

Abbreviations

- C1 - ?quadrate region of rostrum
- C2 - undetermined cartilage, possibly hyomandibula or hyoid
- C3 - part of right scapulocoracoid (?)
- C4 - part of left scapulocoracoid (?)
- cr - circumorbital ridge
- d - denticles
- fc - frontal clasper
- llp - left lower posterior tooth plate («mandibular»)
- MC - Meckel's cartilage
- o - orbit
- oc - occipital cotylus
- or - opercular rays
- r - rostrum
- rlp - right lower tooth plate («mandibular»)
- sc - sagittal crest
- se - sensory canal
- ua - upper anterior tooth plate («vomerine»)
- up - upper posterior tooth plate («palatine»)
- vm - ventral rostral margin

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